A Niche Analysis

of Coexisting *Thais lapillus* and *Urosalpinx cinereus* Populations

BY

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INTRODUCTION

THE MURICID GASTROPODS *Thais lapillus* (Linnaeus, 1758) and *Urosalpinx cinerea* (Say, 1822) inhabit rocky intertidal shores of the northeastern United States. An extensive literature on the food habits of these species documents their principal prey as oysters, clams, mussels and barnacles (*e. g.*, CARRIKER, 1955; CONNELL, 1961a, 1961b; WOOD, 1968; MENGE, 1978a, 1978b). Although these snails feed upon similar prey in rocky intertidal habitats, there are no reports of competitive interactions between *Thais* and *Urosalpinx* populations. This is at least partly because their geographical distributions do not overlap widely. *Urosalpinx* is a native of North America and ranges from Nova Scotia to northeast Florida (ABBOTT, 1974), although populations have been introduced to the British Isles and to the west coast of the United States (WOOD, 1968). *Thais (Nucella) lapillus* is found on western and eastern shores of the North Atlantic Ocean, where it is reported from southern Labrador to New York in North America and from Norway to Portugal in Europe (ABBOTT, *op. cit.*). In North America, their local habitat requirements differ. In the northern extent of its range, *Urosalpinx* is found in isolated populations in sheltered waters (CARRIKER, 1955). North of Cape Cod, Massachusetts, *Thais* is reported from rocky habitats varying in wave exposure from wave swept headlands to sheltered coves (MENGE, 1978a).

The present study provides information on the distribution, abundance and food habits of coexisting *Thais* and *Urosalpinx* populations. Aspects of the feeding niche of these animals are contrasted to gain insight into patterns of resource utilization by both species. These patterns indicate that *Thais* and *Urosalpinx* may compete for prey in certain habitats.

MATERIAL AND METHODS

The study area was located in the town of Narragansett, on the western shore of Rhode Island Sound, approximately 5 km N of Point Judith, Rhode Island (41°25′N; 71°27′W). Three distinct rocky intertidal habitats were present: rock ledge directly exposed to wave action, semiprotected boulders sheltered from direct wave action by offshore rocks and shoals, and a large enclosed tide pool, completely sheltered from wave exposure. The area inhabited by *Thais* and *Urosalpinx* in the tidal pool consisted of an intertidal band extending around the 50 m circumference of the pool. Equal area sampling in the more exposed habitats allowed direct comparison of snail density among habitats. All specimens of *Urosalpinx* and *Thais* inhabiting each of the 3 habitats were counted by sequentially visiting the study area during day time low tide periods from June to August 1975. Snails located on barnacles or mussels were examined for the presence of the proboscis inserted between barnacle opercula, or presence of a drill hole on barnacles or mussels. Snail shell length, mussel shell length and diameter of the basal portion of barnacle tests were measured.

Quadrat sampling was conducted in each habitat to estimate the distribution and abundance of prey species. A 0.25 m^2 quadrat was located along the intertidal zone of each area by placing the corner of the quadrat on coordinates selected from a random number table. Fifty quadrats were censused in the protected tide pool, 30 quadrats in the semiprotected habitat and 20 quadrats in the exposed habitat. Due to increased prey abundances at the more exposed habitat, fewer quadrats were sampled there.

RESULTS

Abundance and Distribution of Predators and Prey

A total of 534 specimens of *Thais* and 339 specimens of *Urosalpinx* was censused over the 8 week period. Both snail species were in similar abundance in protected and semiprotected habitats, but no *Urosalpinx* were found in the exposed habitat, although *Thais* were very abundant there (Table 1). *Urosalpinx* specimens were commonly found individually on open rock faces, whereas *Thais* specimens occurred more often in aggregations numbering 10-30 individuals in crevices and other sheltered locations. The tendency for *Urosalpinx* to occupy relatively unprotected microhabitats may partly explain the absence of these snails from wave swept locations. *Thais* shell length was significantly smaller ($p < 0.05$) in the exposed area than in the tide pool or semiprotected habitats. *Urosalpinx* shells were significantly larger ($p < 0.05$) than *Thais* shells in protected and semiprotected habitats.

Except for one *Urosalpinx* specimen feeding on the snail *Littorina littorea,* both gastropod predators consumed only mussels, *Mytilus edulis* and acorn barnacles, *Balanus balanoides.* Both prey species increased in population density dramatically with increasing wave exposure (Table 2). Using the the variance-to-mean ratio of individuals per quadrat as a measure of spatial dispersion (PIELOU, 1969; ELLIOTT, 1971), barnacles and mussels had strongly clumped distributions (Table 2), with prey

Table 1

Mean size ± std error (cm) and density for *Thais lapillus* and *Urosalpinx cinerea* in three habitats.

Species	Habitat	Shell Length	Number per m²
Thais	protected	1.93 ± .03	2.9
	semiprotected	1.94 ± .02	3.4
	exposed	1.57 ± .02	4.4
Urosalpinx	protected	2.17 ± .02	3.1
	semiprotected	2.25 ± .03	3.6
	exposed	—	0.0

Table 2

Distribution and abundance of *Balanus balanoides* and *Mytilus edulis* in three habitats.

Species	Habitat	Index of Dispersion[1]	Number per 0.25 m²
Balanus	protected	23.1	20.4 ± 3.1
	semiprotected	24.7	40.5 ± 5.8
	exposed	71.0	60.1 ± 14.6
Mytilus	protected	15.2	2.1 ± 0.9
	semiprotected	15.1	14.9 ± 2.7
	exposed	102.2	75.2 ± 19.6

[1](variance/mean)(N−1)

Table 3

Mean prey size ± std error (cm) available and eaten.

Species	Habitat	Prey Size Available	Prey Size Eaten: Thais	N	Urosalpinx	N
Balanus balanoides	protected	.45 ± .01	0.46 ± .04	29	0.44 ± .04	17
	semiprotected	.57± .01	0.33 ± .03[2]	14	0.45 ± .04[2]	23
	exposed	.60 ± .02	0.29 ± .02[2]	26	—	0
Mytilus edulis	protected	2.07 ± .09	2.28 ± .32	9	2.05 ± .17	32
	semiprotected	2.28 ± .09	1.84 ± .23	11	2.66 ± .15	42
	exposed	0.87 ± .03	1.36 ± .11[2]	47	—	0

[2]H_0: $\bar{x}$ drilled $= \bar{x}$ available rejected at $p < 0.05$.

in the exposed habitat showing the greatest degree of aggregation. Chi-square contingency tests for association between mussels and barnacles (PIELOU, *op. cit.*) indicated that the 2 prey species were distributed independently of one another in each habitat. Specimens of *Balanus* increased in size with increasing wave exposure, whereas mussels were moderately large in the protected and semiprotected habitats, and were significantly smaller ($p < 0.001$) in the exposed environment (Table 3).

Prey Sizes Eaten

A total of 250 snails were observed feeding, 114 *Urosalpinx* and 136 *Thais*. The mean size of prey specimens eaten by each snail species in each habitat was contrasted with the mean size of prey available in the same habitat. Single classification analysis of variance showed that barnacles and mussels consumed by either predator in the tide pool were not significantly different from the mean sizes available (Table 3). In the semiprotected habitat, *Thais* and *Urosalpinx* took smaller barnacles than the mean size available, but both predators preyed upon average-sized mussels there. In the exposed habitat, *Thais* ate smaller than average barnacles, and larger than average mussels.

YOSHIYAMA & ROUGHGARDEN (1977) derived a competition function, α, which measures the amount of overlap between 2 species having bivariate gaussian resource utilization functions.

$$\alpha(D_x, D_y) = \exp\left(-\frac{1}{2}\left[\frac{D_x^2}{2\sigma_x^2} + \frac{D_y^2}{2\sigma_y^2}\right]\right)$$

In the present case, D_x is the difference between the mean size of mussels eaten and available, σ_x^2 is the variance in size of mussels, and D_y and σ_y^2 are the differences between the size of barnacles eaten and available, and variance in size of barnacles, respectively. *Urosalpinx* exploited the bivariate resource quite fully in protected and semiprotected habitats (Table 4). *Thais* had a declining overlap with available food sizes as the habitat became progressively more exposed, indicating more pronounced prey size selection in exposed habitats.

YOSHIYAMA & ROUGHGARDEN'S (1977) measure was also used to calculate the niche overlap for prey size between *Thais* and *Urosalpinx*. D_x was the difference between mean size of mussels eaten by *Thais* and *Urosalpinx*, D_y was the difference in barnacle size eaten by the 2 predators, and σ_x^2 and σ_y^2 were as above. The niche overlap was highest (0.98) in the tide pool, but dropped to 0.76 in the semiprotected habitat. The overlap between predatory snails was zero in the exposed habitat because of the absence of *Urosalpinx* there.

Table 4

Thais lapillus and *Urosalpinx cinerea* niche breadth values.

Species	Habitat	Niche Breadth: Bivariate Prey Size[3]	Niche Breadth: Prey Species[4]
Thais	protected	.99	.91
	semiprotected	.31	.87
	exposed	.08	1.00
Urosalpinx	protected	1.00	.92
	semiprotected	.89	1.00
	exposed	–	–

[3]Overlap between prey size eaten and available.
[4]Overlap between prey species eaten and available.

Prey Species Eaten

The degree of preference for each type of prey was investigated by calculating PETRAITIS' (1979) measure of niche breadth:

$$B = (q_1/p_1)^{p_1} \cdot (1-q_1/1-p_1)^{1-p_1}$$

where p_1 is the frequency of barnacles in a predator's diet and q_1 is the frequency of barnacles available in the habitat. The value of B may range from 0 to 1, with smaller values representing ecological specialists using resources in proportions dissimilar to their availability, and larger B values representing ecological generalists using resources in the same proportion they occur in the environment. Prey availability was estimated by assuming that the frequency of encounter of a prey species was proportional to the relative cover of that prey in the habitat. The relative cover of a species was estimated by multiplying the area occupied by an average-sized individual in a given habitat by the density of that species. The niche breadth values showed *Thais* and *Urosalpinx* to be generalist feeders in all habitats, achieving values between 0.87 and 1.0 (Table 4).

The amount of niche overlap between 2 species competing for the same species of prey was measured as the probability that a particular species' utilization curve could have been drawn from that of another species (PETRAITIS, 1979). The specific overlap between *Thais* and *Urosalpinx* is:

$$o_{12} = (p_2/p_1)^{p_1} \cdot (1-p_2)/(1-p_1)^{1-p_1}$$

where p_1 and p_2 are the utilization frequencies of barnacles by *Thais* and by *Urosalpinx,* respectively. The mean overlap ($o_{12} + o_{21}/2$) in the protected, semiprotected and exposed habitats was 0.70, 0.91 and 0.0, respectively. The comparatively low overlap between predators in the tide pool was caused by *Thais* eating somewhat more barnacles and *Urosalpinx* eating fewer barnacles than expected on the basis of prey availability.

DISCUSSION

Species which utilize common resources in the same community are thought to ameliorate the effects of competition via resource partitioning; that is, they subdivide resources on the basis of consumer morphology or behavior (Schoener, 1974). In many communities, similarity of species along one dimension implies dissimilarity along another (*e.g.,* MacArthur, 1958; Schoener, 1970; Cody, 1974). Clearly, *Urosalpinx* and *Thais* eat similar types and sizes of prey, and may show evidence of competition for prey.

Several individuals of each species were maintained on a diet of mussels in a 36 L capacity aquarium for several months. Neither species gave any indication of aggressive interactions, leading one to expect that interference competition (Gill, 1974; Rothstein, 1978) is not important. During periods of low food availability, these snails may compete by a differential ability to locate or consume prey. Competition was most likely in the protected tide pool where the abundance of mussels and barnacles was the lowest. *Thais* and *Urosalpinx* were not selective about which prey size was eaten in that habitat, as demonstrated by the nearly complete overlap between prey size eaten and available. Similarity along the prey size dimension was complemented by dissimilarity along the prey species dimension. *Urosalpinx*'s diet consisted of 35% barnacles and 65% mussels, whereas *Thais* ate 76% barnacles in a habitat where the relative availability of barnacles was 55%.

The substantially greater prey population densities in the semiprotected habitat reduced the likelihood of competition by providing the predators with a large spectrum from which to select. *Thais* and *Urosalpinx* ate smaller barnacles than average, failing to take advantage of the substantially larger barnacles there. Wood (1968) reported that *Urosalpinx* could penetrate the opercular plates of a barnacle and ingest the contents in 20 minutes, whereas if the snail were to drill the barnacle test, several hours would be required. In the present study, *Thais* and *Urosalpinx* fed upon barnacles by drilling and by piercing the operculum, but data on the relative frequency of each method were not recorded. If drilling were a common mode of feeding upon barnacles, drilling smaller barnacles may require less time and shorter periods of exposure to dislodging wave action, favoring predation on smaller than average barnacles in wave swept habitats.

Interspecific competition was zero in the exposed habitat because of the lack of *Urosalpinx* there. Where free of its competitor, *Thais* demonstrated strong prey size selection, but no prey species preference. These data implicate prey size as the more important niche dimension for *Thais*. Experimental studies involving manipulation of *Thais* and *Urosalpinx* densities in various habitats are needed to document the relative importance of competition on prey choice by these predators.

CONCLUSION

I conclude that competition between *Thais* and *Urosalpinx* is most likely along sheltered rocky shores where these predators may reduce the intensity of competition for prey of a given size by feeding preferentially on different prey species. The intensity of competition may be transitory on a seasonal and yearly basis in response to fluctuations in the abundance of predators and prey caused by physical or biological disturbances.

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